

Karyotypes of six populations of *Lycoris radiata* and discovery of the tetraploid

¹ZHOU Shou-Biao * ²YU Ben-Qi ¹LUO Qi ¹HU Jin-Rong ¹BI De

¹(College of Life Sciences, Anhui Normal University, Wuhu, Anhui 241000, China)

²(Anhui University of Technology and Science, Wuhu, Anhui 241000, China)

Abstract Chromosomes and karyotypes are important aspects of plant phylogeny and evolution. The chromosome numbers and karyotypes of *Lycoris radiata* display great variability among and within different populations. By studying different populations of *L. radiata* we acquired some basic data on karyotype evolution and evolutionary mechanisms in *L. radiata* and the genus *Lycoris*. Six populations of *L. radiata* from Anhui and Zhejiang provinces in China were investigated cytologically. The chromosome numbers and karyotype formulae are as follows: Huoshan populations, $2n=44=28st+8t+8T$, $2n=22=6st+12t+4T$; Huangshan populations, $2n=22=22t$, $2n=22=18st+4t$, $2n=21=12st+7t+2T$; Chuzhou population, $2n=33=33t$; Ma'anshan populations, $2n=33=18st+15T$, $2n=25=1m+20st+2t+2T$; Xuancheng populations, $2n=22=20st+2T$, $2n=21=1m+20st$; and Hangzhou populations $2n=22=12st+4t+6T$, $2n=21=18st+3t$. The chromosome numbers and karyotypes of some populations are reported here for the first time and the wild tetraploid population of *L. radiata* was found for the first time. In addition, karyotype evolution among populations and the origin of polyploids are discussed.

Key words *Lycoris radiata*, karyotype, tetraploid.

Lycoris radiata Herb., a member of the Family Amaryllidaceae, is an endemic species in East Asia and is principally native to China, Japan and Korea. It is a very popular bulb flower worldwide with considerable ornamental and medical value. Much work has been done on the karyotypes, morphology, physiology, palynology, and medicinal and molecular aspects (Bose & Flory, 1963; Chen & Hu, 1995; Ren et al., 1995; Zhang & Cao, 2001; Zhang et al., 2002; Nie et al., 2003; Zhou et al., 2005). However, several arguments and problems still remain regarding the cytology of *L. radiata* (Mookerjee, 1955; Shao et al., 1994; Qin et al., 2004a, b; Zhou et al., 2004). This paper focuses on the discovery of some new chromosome numbers and karyotypes when cytological studies were made on different populations of *L. radiata* from Anhui and Zhejiang provinces in East China.

1 Material and methods

All the plant samples studied were collected from the field in Anhui and Zhejiang provinces (Table 1). They were maintained in water culture before their root tips were harvested for the cytological studies. Actively growing root tips were pretreated in p-Dichlorobenzene solution at room temperature for 4 h before they were fixed in Carnoy I (glacial acetic acid: absolute ethanol = 1:3) at 4 °C for 20 h. Then they were macerated in 1 mol/L hydrochloric acid at 60 °C for 2 min, stained in Phenol-Fuchsin solution for 2 h, and squashed in 45% acetic acid.

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* E-mail: <zhoushoubiao@vip.163.com>.

Karyotype formulae are based on the measurements of somatic chromosomes. The symbols used to describe the karyotypes follow Levan et al. (1964): m = median-centromeric chromosome with arm ratio of 1.01–3.00; st = subterminal-centromeric chromosome with arm ratio of 3.01–7.00; t = terminal-centromeric chromosome with arm ratio of over 7.00; and T = terminal-centromeric chromosome with no short arm.

The voucher specimens were deposited in the College of Life Sciences, Anhui Normal University.

Table 1 Origins of materials and the karyotypes of materials studied of *Lycoris radiata*

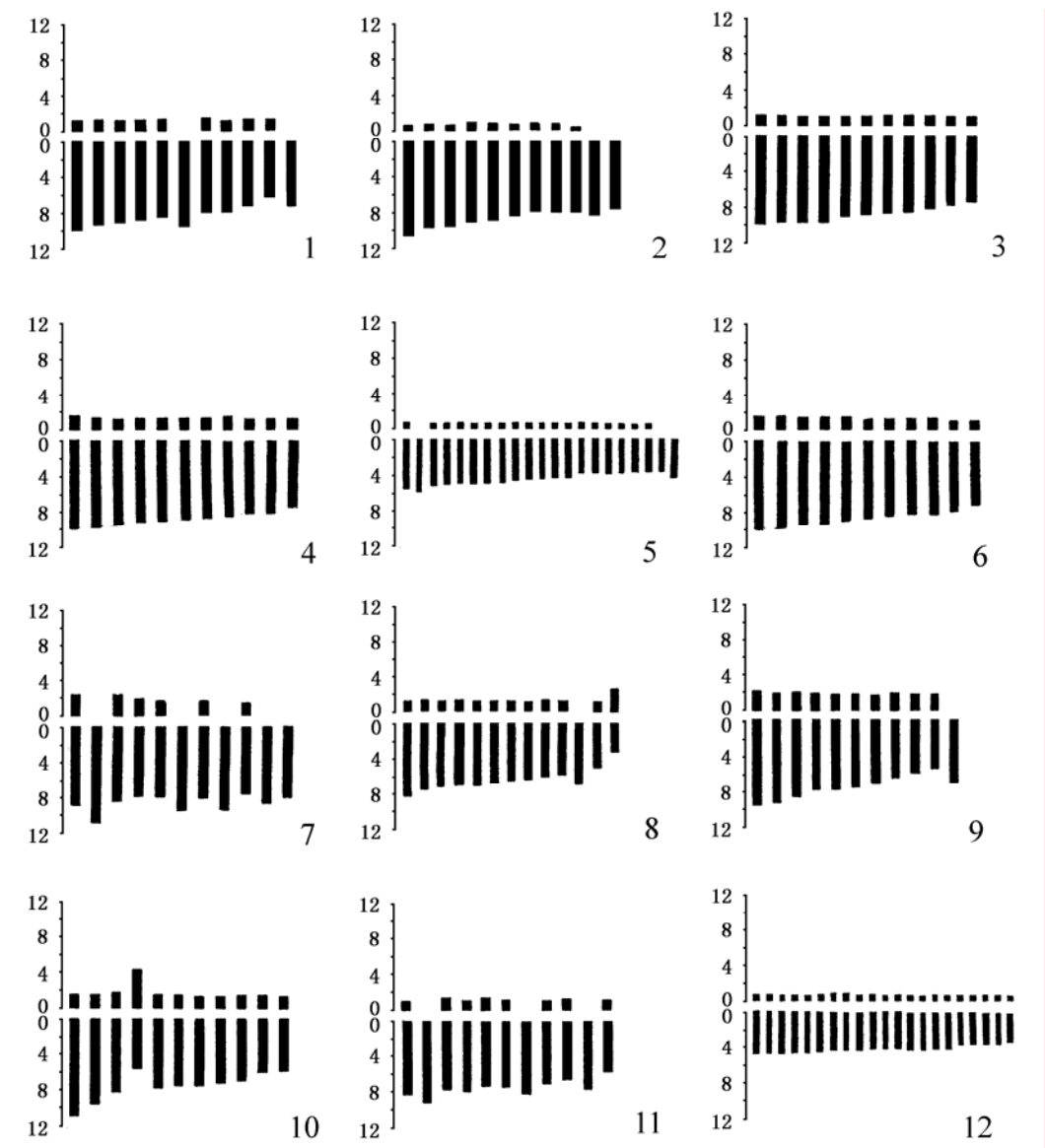
Population		Locality	Karyotypic formula	Type	Voucher
Huoshan	Cytotype I	Longjin Village,	$2n=44=28st+8t+8T$	4A	S. B. Zhou & B.
	Cytotype II	Huoshan, Anhui, China (安徽霍山)	$2n=22=6st+12t+4T$	4A	Q. Yu (周守标, 余本祺) 0301611
Huangshan	Cytotype I	Guniujiang, Huoshan,	$2n=22=22t$	4A	S. B. Zhou & W.
	Cytotype II	Anhui, China	$2n=22=18st+4t$	4A	H. Qin (周守标,
	Cytotype III	(安徽霍山)	$2n=21=12st+7t+2T$	4A	秦卫华) 0301615
Chuzhou		Langyanshan, Chuzhou, Anhui, China (安徽滁州琅琊山)	$2n=33=33t$	4A	S. B. Zhou & B. Q. Yu (周守标, 余本祺) 0401621
Ma'anshan	Cytotype I	Caishiji, Ma'anshan,	$2n=33=18st+15T$	4A	B. Q. Yu & Q.
	Cytotype II	Anhui, China (安徽马鞍山采石矶)	$2n=25=1m+20st+2t+2T$	4A	Luo (余本祺, 罗 琦) 0401617
Xuancheng	Cytotype I	Qingliangfeng, Jixi,	$2n=22=20st+2T$	4A	B. Q. Yu & Y.
	Cytotype II	Xuancheng, Anhui, China (安徽宣城绩溪清凉峰)	$2n=21=1m+20st$	3A	Wang (余本祺, 王影) 0501633
Hangzhou	Cytotype I	Fuyang, Hangzhou,	$2n=21=18st+3t$	4A	S. B. Zhou & W.
	Cytotype II	Zhejiang, China (浙江杭 州富阳)	$2n=22=12st+4t+6T$	4A	H. Qin (周守标, 秦卫华) 0401620

2 Results

2.1 Huoshan population

2.1.1 Cytotype I (Figs. 1, 13) The chromosomes were counted to be $2n=44$ of tetraploid cytotype, which is reported for the first time. The karyotype was formulated as $2n=28st+8t+8T$, consisting of 28 subterminal-centromeric (st), 8 terminal-centromeric (t) and 8 Terminal-centromeric (T). The ratio of the length of the largest chromosome to that of the smallest was 1.53, and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.05–10.82 in relative length. The statistics show that 70% of the cells were tetraploid.

2.1.2 Cytotype II (Figs. 2, 14) The chromosomes were counted to be $2n=22$. The karyotype was formulated as $2n=6st+12t+4T$, consisting of 3 pairs of subterminal-centromeric, 6 pairs of terminal-centromeric, and 2 pairs of Terminal-centromeric. A pair of secondary constriction was observed on the short arms of the ninth chromosome pair, which is reported for the first time. The ratio of the length of the largest chromosome to that of the smallest was 1.52 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.31–11.12 in relative length.



Figs. 1–12. Idiograms of six populations of *Lycoris radiata*. 1. Huoshan population (Cytotype I). 2. Huoshan population (Cytotype II). 3. Huangshan population (Cytotype I). 4. Huangshan population (Cytotype II). 5. Huangshan population (Cytotype III). 6. Chuzhou population. 7. Ma'anshan population (Cytotype I). 8. Ma'anshan population (Cytotype II). 9. Xuancheng population (Cytotype I). 10. Xuancheng population (Cytotype II). 11. Hangzhou population (Cytotype I). 12. Hangzhou population (Cytotype II).

2.2 Huangshan population

2.2.1 Cytotype I (Figs. 3, 15) The chromosomes were counted to be $2n=22$ of normal diploid cytotype. They were arranged in 11 groups of 2 homologues. All were terminal-centromeric. The karyotype was formulated as $2n=22t$. The ratio of the length of the largest chromosome to that of the smallest was 1.33 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 8.45–11.20 in relative length.



Figs. 13–18. Karyotypes of six populations of *Lycoris radiata*. **13.** Huoshan population (Cytotype I). **14.** Huoshan population (Cytotype II). **15.** Huangshan population (Cytotype I). **16.** Huangshan population (Cytotype II). **17.** Huangshan population (Cytotype III). **18.** Chuzhou population.

2.2.2 Cytotype II (Figs. 4, 16) The chromosomes were counted to be $2n=22$, consisting of 9 pairs of subterminal-centromeric and two pairs of terminal-centromeric. The karyotype was formulated as $2n=18st+4t$. The ratio of the length of the largest chromosome to that of the smallest was 1.41 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.64–10.79 in relative length.

2.2.3 Cytotype III (Figs. 5, 17) The chromosomes were counted to be $2n=21$, consisting of 12 subterminal-centromeric, 7 terminal-centromeric and 2 Terminal-centromeric. The karyotype was formulated as $2n=12st+7t+2T$. The ratio of the length of the largest chromosome to that of the smallest was 1.52 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 3.85–5.86 in relative length.

2.3 Chuzhou population (Figs. 6, 18)

The chromosomes were counted to be $2n=33$ of normal triploid cytotype. All of them were subterminal-centromeric. The karyotype was formulated as $2n=33t$. The ratio of the length of the largest chromosome to that of the smallest was 1.52 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.10–10.80 in relative length.

2.4 Ma'anshan population

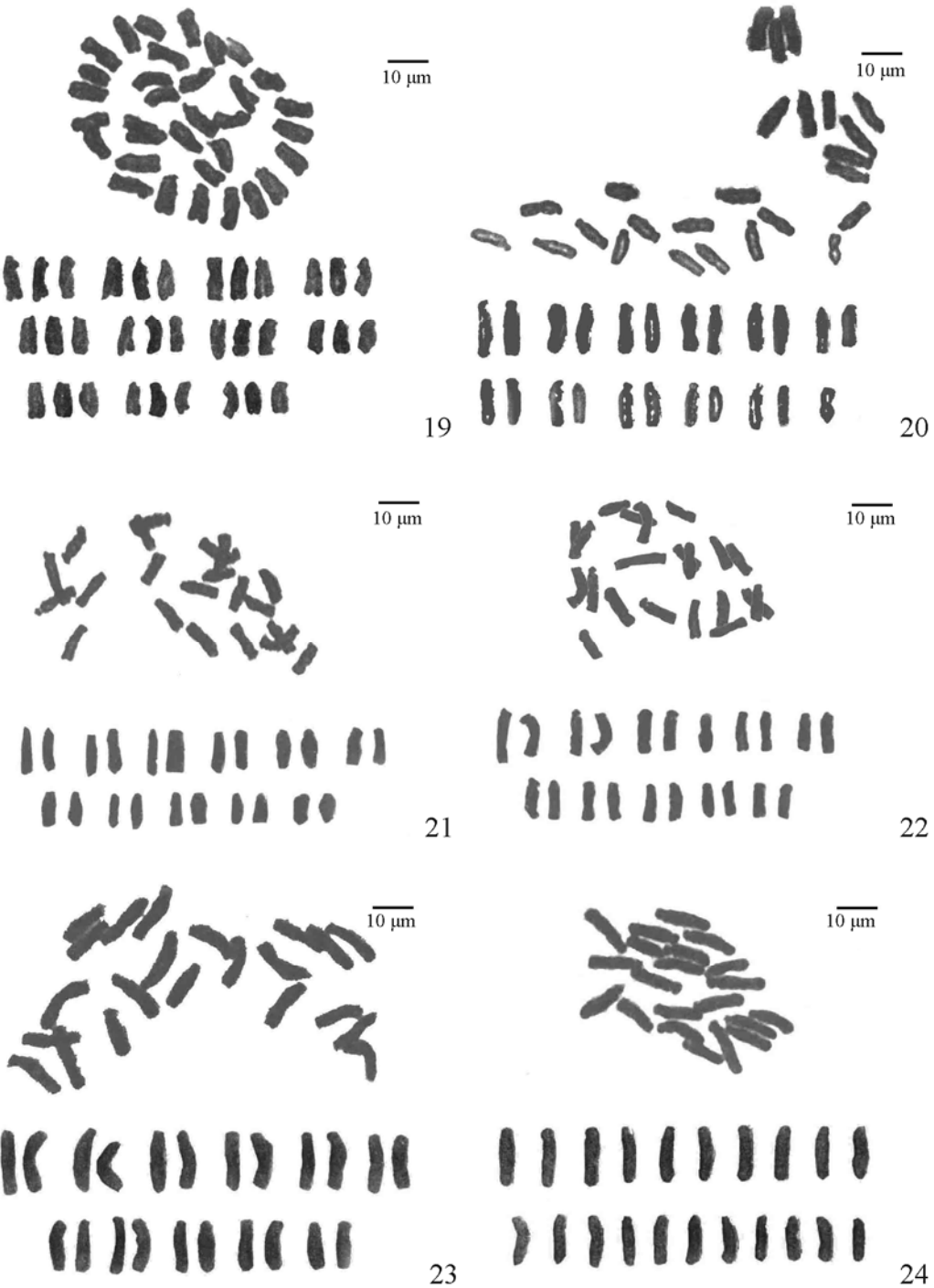
2.4.1 Cytotype I (Figs. 7, 19) The chromosomes were counted to be $2n=33$, which is reported for the first time. They consisted of 18 subterminal-centromeric and 15 Terminal-centromeric. The karyotype was formulated as $2n=18st+15T$. The ratio of the length of the largest chromosome to that of the smallest was 1.43 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.59–10.84 in relative length.

2.4.2 Cytotype II (Figs. 8, 20) The chromosomes were counted to be $2n=25$, which is first reported. They consisted of 1 metacentric-centromeric (m), 20 subterminal-centromeric, 2 terminal-centromeric and 2 Terminal-centromeric. The karyotype was formulated as $2n=1m+20st+2t+2T$. The ratio of the length of the largest chromosome to that of the smallest was 1.58 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 4.49–5.99 in relative length. The statistics show that 40% of the cells were of this cytotype.

2.5 Xuancheng population

2.5.1 Cytotype I (Figs. 9, 21) The chromosomes were counted to be $2n=22$, which is first reported. They consisted of 10 pairs of subterminal-centromeric and 1 pair of Terminal-centromeric. The karyotype was formulated as $2n=20st+2T$. The ratio of the length of the largest chromosome to that of the smallest was 1.57 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.20–11.30 in relative length.

2.5.2 Cytotype II (Figs. 10, 22) The chromosomes were counted to be $2n=21$, which is first reported. They consisted of 1 metacentric-centromeric and 10 pairs of subterminal-centromeric. The karyotype was formulated as $2n=1m+20st$. The ratio of the length of the largest chromosome to the smallest was 1.69 and the proportion of chromosomes with arm ratio $>2:1$ was 0.95. The karyotype was therefore of 3A type according to the degree of



Figs. 19–24. Karyotypes of six populations in *Lycoris radiata*. **19.** Ma'anshan population (Cytotype I). **20.** Ma'anshan population (Cytotype II). **21.** Xuancheng population (Cytotype I). **22.** Xuancheng population (Cytotype II). **23.** Hangzhou population (Cytotype I). **24.** Hangzhou population (Cytotype II).

asymmetry and the chromosomes ranged from 7.13–12.02 in relative length. The statistics show that 47% of the cells were of this cytotype.

2.6 Hangzhou population

2.6.1 Cytotype I (Figs. 11, 23) The chromosomes were counted to be $2n=22$, which is first reported. They consisted of 6 pairs of subterminal-centromeric, 2 pairs of terminal-centromeric and 3 pairs of Terminal-centromeric. The karyotype was formulated as $2n=12st+4t+6T$. The ratio of the length of the largest chromosome to the smallest was 1.36 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 7.44–11.12 in relative length. The statistics show that 50% of the cells were of this abnormal diploid.

2.6.2 Cytotype II (Figs. 12, 24) The chromosomes were counted to be $2n=21$, which is first reported. They consisted of 18 subterminal-centromeric and 3 terminal-centromeric. The karyotype was formulated as $2n=18st+3t$. The ratio of the length of the largest chromosome to the smallest was 1.46 and the proportion of chromosomes with arm ratio $>2:1$ was 1.0. The karyotype was therefore of 4A type according to the degree of asymmetry and the chromosomes ranged from 3.74–5.47 in relative length.

3 Discussion

There have been numerous cytological studies on *L. radiata* on a worldwide basis (Nishiyama, 1928; Inariyama, 1931, 1951a, b; Mookerjee, 1955; Takemura, 1962a, b; Bose & Flory, 1963; Yoshida, 1972; Nishikawa et al., 1979; Xu et al., 1984; Chen & Li, 1985; Kurita, 1987, 1988, 1989; Liu & Xu, 1989; Shao et al., 1994; Sun et al., 1998). The results show that: *L. radiata* is a complex which includes not only the diploid ($2n=22=22t$) but also the triploid ($2n=33=33t$). The basic chromosome number of *L. radiata* is $x=11$. The usual karyotype of *L. radiata* consists only of rod chromosomes with subterminal or terminal constriction (with only one arm). However, several studies (Mookerjee, 1955; Bose, 1963; Xu et al., 1984; Chen & Li, 1985; Kurita, 1987, 1988; Shao et al., 1994; Qin et al., 2004a, b; Zhou et al., 2004) have found some abnormal karyotypes of *L. radiata* such as $2n=33=1m+31t+1B$, $2n=32=1m+31t$ (Bose, 1963; Kurita, 1987, 1988); $2n=22=4st+18t$ (Chen & Li, 1985; Sun et al., 1998); $2n=33=15t+18st$ (Xu et al., 1984); $2n=23=6st+14t+2T+1B$, $2n=22=1m+12st+8t+1B$ (Shao et al., 1994); $2n=24=6m+8sm+6st+4t$ (Qin et al., 2004a); and $2n=21=1m+6st+4t+9T+1B$, $2n=21=1M+10st+9T+1B$ (Zhou et al., 2004). In addition, Qin et al. (2004b) observed long oval chromosomes. The new chromosome numbers and karyotypes found in our studies are different from those in other reports. A tetraploid cytotype of *L. radiata* was found here for the first time and in the field observations their tepals did not recurve and the margins did not undulate, very distinct from other populations. Secondary constriction in the Huoshan population was found for the first time and different cytotypes were found in the same population. It was therefore concluded that the chromosome numbers and karyotypes of *L. radiata* vary in different populations and even within the same population.

According to most studies (for example Inariyama, 1953; Stebbins, 1971; Jones, 1976; Xu et al., 1984), the karyotype evolution of the genus *Lycoris* is mainly decided by Fusion Theory which holds that the basic chromosome number of the genus is $x=11$ and that the species with rod chromosomes ($2n=22t$ or $2n=33t$) are primitive taxa. Two rod chromosomes with terminal constrictions format an m chromosome (large M chromosome) through the fusion of constrictions and reciprocal translocation of Robertson Change. In contrast, a few studies (Bose & Flory, 1963; Jones, 1978) agree that the karyotype evolution of the genus *Lycoris* is mainly decided by Fission Theory. According to this theory the chromosome group

of the original species of the genus *Lycoris* should be $2n=12M$, which consists of 12 large M chromosomes with median constrictions. It is also believed that the basic chromosome number of the genus is $x=6$ and one M chromosome could be divided into two t or T chromosomes through the fission of constrictions and reciprocal translocation of Robertson Change (Lincoln & Clark, 1982; Hong, 1990). One crucial index to testify Robertson Change is whether or not groups of chromosomes with different chromosome numbers have the same number of long arms. Nowadays most of the researchers agree that although the chromosome numbers and karyotypes vary dramatically in *L. radiata*, the total number of arms of a chromosome complement of any species is always a multiple of 11. However, the new formulas of the 6 populations in the present study are difficult to explain by the Fusion Theory or the Fission Theory. Further research on karyotype evolution of *L. radiata* will therefore be needed in the future.

Mookerjea (1955) found that the chromosome number of *L. radiata* was very variable from $2n=15, 22, 25$ to $2n=32$, and it also consisted of m chromosomes (with median of submedian constrictions) and the chromosomes with satellite chromosomes. Because she could not explain the great variability on the chromosome number of *L. radiata*, her opinion did not gain sufficient attention at that time. Through our studies of the 6 populations of *L. radiata*, we agree with Mookerjea that the chromosome numbers and karyotype in *L. radiata* have great variability among different populations and even within the same population. The origin of the karyotype of *L. radiata* is whether gene mutation was caused by the environment or other reasons, so considerable effort will need to be expended in further investigations. This paper can only present some basic data on karyotype evolution in *L. radiata* and the genus *Lycoris*.

The theory of the origin of the *L. radiata* triploids is challenged by the new discoveries in the present study. There are two key hypotheses on the origin of the triploids in the genus *Lycoris*. The first is that they are derived from the hybridization of diploids with tetraploids and the second is that they are derived from the combination between an unreduced gamete of a diploid and a normal gamete of another diploid. Because *L. radiata* has been proven to be an autotriploid by Inariyama (1931) and the tetraploids have never been found (Chung, 1999), nowadays most researchers agree to the latter explanation. However, this is also questioned by the new discovery of tetraploid cytotype and secondary constriction in the Huoshan population and new karyotypes in other populations. Whether or not the triploids derive from the hybridization of diploids with tetraploids is a question which needs further investigation of allozyme, molecular, and hybridization *in situ* methods.

Lycoris radiata seeds are often difficult to germinate and the seedlings take about ten years to reach flowering size. Therefore these plants have usually been produced by clonal propagation. For example, Chung (1999) found that eight sampled populations of *L. radiata* across South Korea were a single clone that had been spread and planted by bulb division. This has allowed the spread of sterile triploids at the expense of less attractive wild types. Both the wild and cultivated plants were propagated by splitting their bulbs. The seeds of diploids and tetraploids are sterile and the seed setting percentage was rather low, and the triploids were fully sterile. Whether or not the wild tetraploids could display amphigenesis needs further detailed study.

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六个石蒜居群的核型及四倍体石蒜的发现

¹周守标* ²余本祺 ¹罗琦 ¹胡金蓉 ¹毕德

¹(安徽师范大学生命科学学院 芜湖 241000)

²(安徽工程科技学院 芜湖 241000)

摘要 染色体与核型的变化是植物系统发育和进化的一个重要方面。石蒜属 *Lycoris* 植物特别是石蒜 *L. radiata* 在染色体数目和核型上存在较大的变异。通过对不同居群的石蒜核型研究, 可以为石蒜和石蒜属植物的核型演化及演化机制提供一些重要的基础资料。本文对分布于中国安徽省和浙江省的6个石蒜居群进行了细胞学研究。结果表明, 6个石蒜居群的染色体数目和核型分别为: 霍山居群 $2n=44=28st+8t+8T$, $2n=22=6st+12t+4T$; 黄山居群 $2n=22=22t$, $2n=22=18st+4t$, $2n=21=12st+7t+2T$; 滁州居群 $2n=33=33t$; 马鞍山居群 $2n=33=18st+15T$, $2n=25=1m+20st+2t+2T$; 宣城居群 $2n=22=20st+2T$, $2n=21=1m+20st$; 杭州居群 $2n=22=12st+4t+6T$, $2n=21=18st+3t$ 。其中, 部分居群的核型类型为首次报道; 并首次发现了四倍体的石蒜居群。此外, 对石蒜的核型进化和多倍体起源进行了初步探讨。

关键词 石蒜; 核型; 四倍体